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LATE QUATERNARY ARTHROPODS FROM THE COLORADO PLATEAU, ARIZONA AND UTAH

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ABSTRACT—Late Quaternary-age arthropods were recovered from dry cave deposits and packrat middens located in the Grand Canyon, Canyonlands, and Glen Canyon region of the Colorado Plateau. This Quaternary data resource has not been analyzed before from the Colorado Plateau national parks. Radiocarbon dates on the various deposits containing arthropods range from 1510 to 30,660 yr B.P. The fossil assemblages yielded 57 identified taxa of insects, arachnids, and millipedes, including 15 taxa taken to the species level. The information from the fossil insect record of the Colorado Plateau is not yet sufficiently detailed to permit precise paleoenvironmental reconstructions. However, preliminary conclusions suggest a cooler, moister climatic regime during the late Wisconsin glacial and a mosaic of vegetation types, such as grassland and shrubby communities, unlike the present vegetation at the localities.

Key words: Quaternary, Colorado Plateau, arthropods, Wisconsin glacial, Grand Canyon, caves.

This paper discusses the results of a preliminary study of late Quaternary arthropod fossils from cave deposits and packrat middens from southern Utah and northern Arizona. This Quaternary data source has not been analyzed before from the Colorado Plateau, although the arid Southwest has been the focus of paleoenvironmental studies for approximately half a century (Antevs 1939). Arid climate, coupled with episodic fluctuating water tables, has proven detrimental to the preservation of most exposed fossil remains. However, the same xeric conditions, when coupled with a stable rock shelter, provide a unique situation—dry preservation. Such xeric locations provide the preservation of not only pollen and plant macrofossils, but also soft tissues and other usually degradable remains of animals (such as skin, hair, keratinous tissues, and dung; Wilson 1942). The study of packrat middens in the Southwest has provided a reconstruction of the Wisconsin glacial biological communities never before observable in such detail (see various chapters in Betancourt et al. 1990). Thus, an entirely new field of research has been opened, and it should prove valuable in understanding the latest Pleistocene.

Dry cave deposits were quickly discovered to be a warehouse of late Pleistocene information. Gypsum Cave (near Las Vegas, Nevada) and Rampart Cave (western Grand Canyon, Arizona) were the scenes of the first paleoecological studies utilizing dry-preserved dung of an extinct animal. Laudermilk and Munz (1934, 1938) found a wealth of information preserved in the dung of extinct Shasta ground sloth (*Nothrotheriops shastensis*). Later studies concerned with dietary reconstructions expounded on the data available from dung of extinct herbivores, including Shasta ground sloth, mammoth (*Mammuthus*), Harrington's mountain goat (*Oreamnos harringtoni*), and bison (*Bison*), among others (Martin et al. 1961, Hansen 1980, Davis et al. 1984, Mead, O'Rourke, and Foppe 1986, Mead, Agenbroad et al. 1986, Mead et al. 1987, Mead and Agenbroad 1989).

Packrats (*Neotoma;* Rodentia; Cricetidae) build nests surrounded by construction materials collected from within 30 to 100 m of the house. The construction components are predominantly plant materials, but the packrat also collects small stones, skeletal remains, and dung. Adding to the materials procured by the packrat are various vertebrates and invertebrates who live in the nest and waste pile as commensals. Periodic house cleaning produces a waste pile of debris. Urination on the waste pile (a midden) ultimately may cement the remains into a rock-hard deposit, encapsulating

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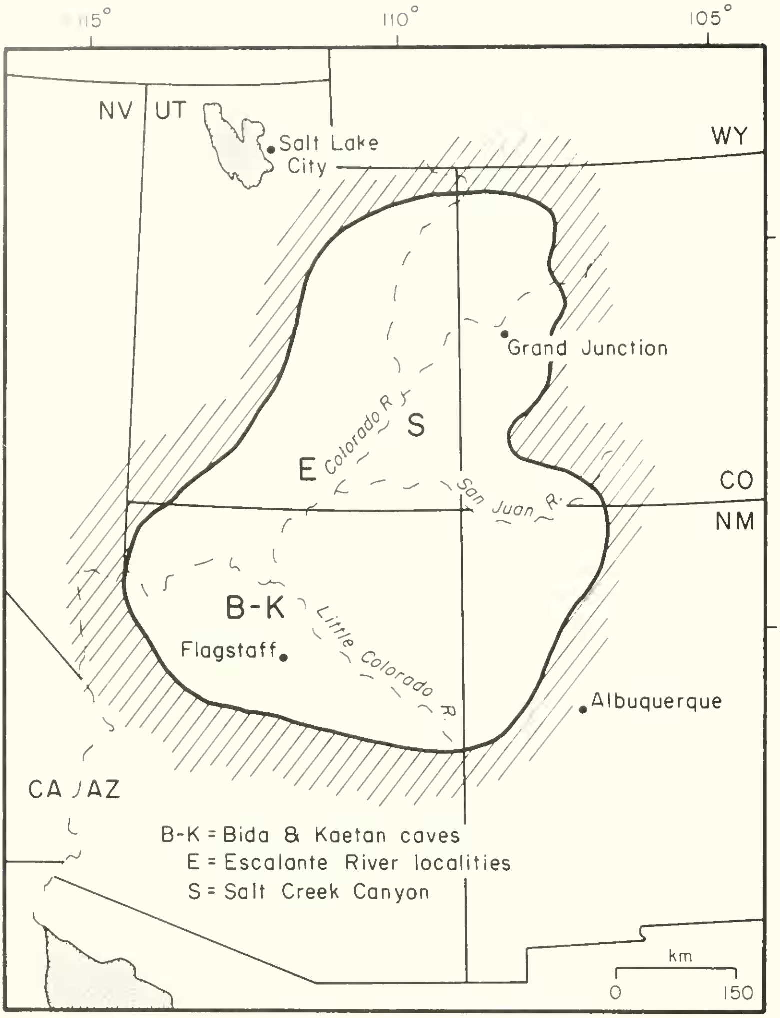

Fig. 1. Map of the Colorado Plateau with sites discussed in text.

the contents of that time. When these indurated (cemented) middens are located in a dry alcove, rock shelter, or cave, the contents may be preserved for as long as the shelter exists. Radiocarbon dating of indurated midden layers provides a chronological framework for the associated plant and animal remains. Middens, then, provide a unique examination of local past biotic communities.

The investigation of insect fossils from ancient packrat middens and cave deposits is a new approach that is just beginning to show substantial results. One of the authors (SAE) recently performed more extensive research on a series of insect fossil assemblages from packrat middens in the Chihuahuan desert regions of western Texas and south central New Mexico (Elias 1987, Elias and Van Devender 1990, 1991). Elias (1990) also recently published the results of a taphonomic study designed to reveal the sources and possible biases of insect exoskeletons in packrat middens.

METHODS

Localities

Matrices from packrat middens and cave sediments were washed or hand picked for arthropod and other animal and plant remains. Packrat midden and cave deposits from two cave sites were analyzed from Grand Canyon National Park (GRCA), Coconino County, Arizona; three packrat middens from Salt Creek, Canyonlands National Park (CANY), San Juan

County, Utah; and three packrat middens and one cave deposit from the Escalante River region of Glen Canyon National Recreation Area (GLCA), Kane County, Utah (Fig. 1).

Bida Cave is a large limestone cave located in pinyon-juniper woodland at 1430 m elevation in GRCA. Cole (1990) reported on the packrat middens recovered from the cave. Test pit excavations produced a multitude of faunal and floral remains (Mead 1983, O'Rourke and Mead 1985, Mead, O'Rourke, and Foppe 1986, McVickar and Mead ms). Radiocarbon dates (spanning from 2960 to 24,190 yr B.P.) on various remains are presented in Mead (1983) and Mead, Martin et al. (1986); those ages from units containing arthropod remains are listed in Table 1.

Kaetan Cave is a medium-sized limestone cave at 1430 m elevation in GRCA. Mead (1983) excavated portions of the deposit in the entrance room for the remains of extinct mountain goat (*Oreamnos harringtoni*) (O'Rourke and Mead 1985, Mead, O'Rourke, and Foppe 1986). Paleoenvironmental reconstruction based on the macrobotanical remains recovered from packrat middens and stratified sediments is in manuscript (McVickar and Mead). Radiocarbon ages span the period from 14,220 to 30,600 yr B.P. (Table 1).

Three packrat middens selected from a series collected from Salt Creek Canyon, CANY (1505 to 1755 m elevation), have radiocarbon ages spanning 3830 to 27,660 yr B.P.; today the region is pinyon-juniper woodland with sagebrush flats. The analysis of the macrobotanical remains and paleoenvironmental reconstructions of the middens is in manuscript (Mead and Agenbroad).

Bechan Cave contains copious remains of extinct herbivore dung (Davis et al. 1985, Mead, Agenbroad et al. 1986, Mead and Agenbroad 1989) recovered from floor sediments dating 11,600 to 13,505 yr B.P. Arthropods were recovered from the dung layer and from an isolated Holocene-age packrat midden in the cave (Table 1). Other nearby packrat middens contained additional arthropod remains dating from 1510 to 8640 yr B.P.

TABLE 1. Late Quaternary deposits and radiocarbon dates from sites on the Colorado Plateau containing arthropods.

Locality	^{14}C age	Lab number
Grand Canyon National Park, Arizona		
Bida Cave		
Layer 2	2960 ± 200	A-2836
Layer 4	16,150 ± 600	RL-1135
Layer 5	none	—
Layer 8	24,190 + 4300 − 2800	A-2373
Kaetan Cave		
Layer 1	14,220 ± 320	A-2835
Layer 3	17,500 ± 300	A-2723
Layer 5	none	—
Layer 6	30,600 ± 1800	A-2722
Layer 8+	none	—
Packrat midden 1b	17,100 ± 500	A-2719
Owl Roost		
R2	21,430 ± 1500	A-3082
2	none	—
Canyonlands National Park, Utah		
Salt Creek Canyon (packrat middens)		
Dead Owl 1A	3830 ± 70	Beta-18267
Woodenshoe 1	6980 ± 120	Beta-27214
Hoodoo 1	27,660 ± 340	Beta-27213
Glen Canyon National Recreation Area, Utah		
Escalante River region (packrat middens)		
Bechan Cave 3	1510 ± 60	Beta-23706
Cow-Perfect 1	1820 ± 100	Beta-23711
Bowns 1	8640 ± 140	Beta-23704
Bechan Cave 158	11,600–13,505	°

° A series of dates are analyzed on *Mammuthus* (mammoth) and cf. *Euceratherium* (shrub ox) dung (see Davis et al. 1985, Mead, Agenbroad et al. 1986, Mead and Agenbroad ms).

Insects

Fossil insect sclerities were sorted from washed packrat middens and cave sediment matrices. Robust specimens were mounted on modified micropaleontological cards with gum tragacanth, a water-soluble glue. Fragile specimens and duplicates were stored in vials of alcohol. Fossils were identified chiefly through comparisons with modern identified specimens in the U.S. National Museum of Natural History (Smithsonian Institution), Washington, D.C. Some specimens were referred to taxonomic specialists, as noted in the acknowledgments. Modern ecological requirements and distributions for species identified in the fossil assemblages were compiled from the literature and from specimen labels in the U.S. National Museum. All specimens will be curated in the National Park Service Repository, Laboratory of Quaternary Paleontology, Quaternary Studies Program, Northern Arizona University.

Results

The fossil assemblages yielded 57 identified taxa of insects, arachnids, and millipedes, including 15 taxa taken to the species level. Table 2 shows the taxa identified from the

TABLE 2. Fossil arthropods identified from Bida and Kaetan caves, GRCA, Arizona, in minimum number of individuals per sample.

	Bida Cave				Kaetan Cave					
Taxon	2[a]	4	5	8	1[b]	5	8	ORR2[c]	OR2[d]	1b[e]
COLEOPTERA										
CARABIDAE										
Calosoma cf. *scrutator* Fab.	1	—	—	—	—	—	—	—	—	—
Agonum (*Rhadine*) *perlevis* Csy.	2	—	—	—	—	—	—	—	—	—
Agonum (*Rhadine*) sp.	—	1	1	—	—	—	—	—	—	—
SCARABAEIDAE										
Aphodius nr. *ruficlarus* Fall	—	—	—	1	—	—	—	—	—	—
Aphodius sp.	—	—	—	1	—	—	—	—	—	—
Onthophagus sp.	—	—	—	1	—	—	—	—	—	—
Serica sp.	1	—	—	—	—	1	—	2	1	—
Phyllophaga sp.	—	—	1	—	—	—	—	1	—	—
Diplotaxis sp.	1	—	—	—	—	—	—	1	—	—
Genus indeterminate	1	—	—	—	—	1	—	1	—	—
SILPHIDAE										
Thanatophilus truncatus Say	1	—	—	—	—	—	—	—	—	—
PTINIDAE										
Ptinis ap.	—	—	—	—	—	—	—	1	—	—
Niptus cf. *ventriculus* LeC.	—	—	—	—	10	1	—	9	—	4
NITIDULIDAE										
Genus indeterminate	—	—	—	—	—	1	—	—	—	—
DERMESTIDAE										
Genus indeterminate	—	—	1	—	1	—	—	1	—	—
HISTERIDAE										
Genus indeterminate	—	1	—	—	—	—	—	—	—	—
ELATERIDAE										
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
TENEBRIONIDAE										
Eleodes cf. *nigrina* LeC.	—	—	—	—	1	—	—	4	—	—
Eleodes spp.	1	1	1	—	1	4	2	4	1	1
Coniontis sp.	—	—	—	—	—	1	—	—	—	—
MELOIDAE										
Genus indeterminate	—	—	—	1	—	—	—	—	—	—
MELANDRYIDAE										
Anaspis rufa Say	—	—	—	1	—	—	—	—	—	—
CHRYSOMELIDAE										
Lema trilinea White	—	—	—	—	—	1	—	—	—	—
Chaetocnema sp.	1	—	—	—	—	—	—	—	—	—
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
CLERIDAE										
Acanthoscelides sp.	—	—	—	—	—	—	—	1	—	—
CURCULIONIDAE										
Sapotes sp.	—	—	1	—	—	—	—	—	—	—
Ophryastes sp.	—	2	—	1	—	—	—	—	—	—
Scyphophorus acupunctatus Gyll.	2	1	1	—	—	—	—	—	—	—
Orimodema protracta Horn	1	—	—	—	—	—	—	—	—	—
Cleonidius trivittatus or *C. quadrilineatus*	—	1	1	—	—	—	—	—	—	—
Apleurus angularis (LeC.)	—	1	—	—	—	—	—	—	—	—
Genus indeterminate	—	1	1	1	—	—	—	—	—	—
SCOLYTIDAE										
Genus indeterminate	—	—	—	1	—	—	—	—	—	—
NEUROPTERA										
MYRMELEONTIDAE										
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
HOMOPTERA										
CICADIDAE										
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
HEMIPTERA										
Genus indeterminate	—	—	—	—	—	—	—	—	1	—

TABLE 2 CONTINUED.

	Bida Cave				Kaetan Cave					
Taxon	2[a]	4	5	8	1[b]	5	8	ORR2[c]	OR2[d]	1b[e]
ORTHOPTERA										
ACRIDIDAE										
Genus indeterminate	—	1	—	—	—	—	—	—	—	—
LEPIDOPTERA										
Genus indeterminate	—	—	—	1	—	—	—	—	—	—
HYMENOPTERA										
APOIDEA										
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
DIPTERA										
Genus indeterminate	2	—	2	—	—	—	—	—	—	8
ARACHNIDA										
ACARI										
IXODIDAE										
Dermacentor andersoni Stiles	—	2	—	—	1	—	—	—	—	—
Dermacentor sp.	—	—	—	—	—	—	—	—	1	—
SCORPIONIDA										
BUTHIDAE										
Centuroides sp.	—	—	—	1	—	—	—	—	—	—
DIPLOPODA										
Genus indeterminate	—	1	1	—	—	—	—	—	—	—

[a]Numbers refer to layer numbers at Bida Cave.
[b]Numbers refer to layer numbers at Kaetan Cave.
[c]Owl Roost R2.
[d]Owl Roost 2.
[e]Packrat midden 1b.

Grand Canyon region, and Table 3 lists taxa identified from Glen Canyon. The assemblages are dominated by taxa still found today in the American Southwest, but many of the Pleistocene assemblages contain species that live today at elevations higher than the fossil localities. As in other packrat midden and cave assemblages from the American Southwest, the fossil faunas are dominated by a few families of insects and arachnids. The beetle (Coleoptera) families Carabidae (ground beetles), Curculionidae (weevils), Ptinidae (spider beetles), Scarabaeidae (dung beetles and chafers), and Tenebrionidae (darkling beetles) were represented in most assemblages. A few packrat and other mammalian parasites were found, including a tick (Ixodidae) and a blood-sucking bug (Reduviidae) that are known to parasitize packrats in their nests. A number of the identified species merit individual discussion.

Discussion of Selected Species

The ground beetles from the fossil assemblages include both cave dwellers and open-ground species. The caterpillar hunter, *Calosoma scrutator*, was found in a late Holocene assemblage from the Grand Canyon (Table 2). This beetle is widespread in the United States, southern Canada, and northern Mexico (Gidaspow 1959). It has been collected from the floor of Havasu Canyon, GRCA (Elias, unpublished data). The cave beetle, *Agonum perlevis* (Fig. 2A), preys on other arthropods. It is relatively common in caves and near the mouths of mammal burrows. It is found today from the state of Chihuahua, Mexico, northwest to southern Arizona (Barr 1982). This species, found in late Holocene assemblages in both the GLCA and GRCA regions, was identified from Holocene packrat middens from sites in the Chihuahuan desert region of Mexico (Elias and Van Devender, unpublished data). Another ground beetle from the late Holocene record at GLCA is *Discoderus impotens*, which lives in open country. It is common throughout the American Southwest and is found in the Chihuahuan, Sonoran, and Mojave deserts.

The checkered beetle (Cleridae), *Cymatodera pallida* (Fig. 2E), is a predator of bark beetles in coniferous forests in the Chiricahua, Rincon, and Huachuca mountains of Arizona, as well as in mountainous regions of Chihuahua, Mexico (Vaurie 1952). *C. pallida* was found in a late Pleistocene sample from the Grand Canyon.

The dung beetle (Scarabaeidae), *Aphodius ruficlarus*, was found in a late Pleistocene

TABLE 3. Fossil arthropods identified from the Canyonlands and Glen Canyon region, Utah, in minimum number of individuals per sample.

Taxon	CANY[a]			GLCA[b]			
	DO1A[c]	WS1	HD1	BC3[d]	C-P1	B1	BC15S
COLEOPTERA							
CARABIDAE							
Agonum (Rhadine) perlevis Csy.	—	—	—	2	—	—	—
Amara sp.	—	1	—	—	—	—	—
Discoderus impotens LeC.	—	—	—	1	—	—	—
Genus et sp. indeterminate	—	1	—	1	—	—	—
SCARABAEIDAE							
Aphodius spp.	—	—	—	—	—	—	2
Ataenius sp.	—	—	—	—	—	—	2
Serica sp.	—	—	—	1	—	—	—
Melolontha sp.	—	—	—	—	—	—	1
Diplotaxis sp.	—	—	—	1	—	—	—
Genus et sp. indeterminate	—	1	—	—	—	—	—
PTINIDAE							
Niptus sp.	10	—	1	1	—	2	—
Ptinus spp.	—	—	—	1	—	—	—
ELATERIDAE							
Genus et sp. indeterminate	—	2	—	—	1	—	—
BYRRHIDAE							
Genus et sp. indeterminate	—	—	—	—	1	—	—
TENEBRIONIDAE							
Eleodes spp.	—	—	1	1	—	—	—
Coniontis sp.	—	—	—	1	—	—	—
Genus et sp. indeterminate	1	—	—	—	—	—	—
DERMESTIDAE							
Genus et sp. indeterminate	1	—	—	—	—	—	—
CHRYSOMELIDAE							
Altica sp.	—	—	—	—	—	1	—
Pachybrachis sp.	—	1	—	—	—	—	—
Genus et sp. indeterminate	—	1	—	—	—	—	—
CLERIDAE							
Cymatodera pallida Schffr.	—	—	—	—	—	—	1
HOMOPTERA							
REDUVIIDAE							
Triatoma sp.	—	—	—	1	—	—	—
LEPIDOPTERA							
Genus et sp. indeterminate	—	—	1	—	—	—	—
HYMENOPTERA							
FORMICIDAE							
Formica sp.	1	—	—	—	—	—	—

[a]CANY = Canyonlands National Park
[b]GLCA = Glen Canyon National Recreation Area
[c]Sites in Canyonlands are DO1A, Dead Owl 1A; WS1, Woodenshoe 1; HD1, Hoodoo 1
[d]Sites in Glen Canyon are BC3, Bechan Cave 3; C-P1, Cow Perfect 1; B1, Bowns 1; BC15S, Bechan Cave 15S

assemblage from GLCA. This beetle lives today throughout much of western North America from Saskatchewan in the north to New Mexico, Arizona, and California in the south. At the southern limit of its range, it lives in mountainous regions.

The carrion beetle (Silphidae), *Thanatophilus truncatus* (Fig. 2B), lives in the southwestern U.S. and northern Mexico in habitats spanning altitudinal gradients from grasslands and arid scrub desert through oak-pinyon-juniper woodlands, pine forests, and montane meadows (Peck and Kaulbars 1987). *T. truncatus* was found only in a late Holocene assemblage from the Grand Canyon.

The spider beetle (Ptinidae), *Niptus ventriculus*, is a scavenger that ranges from Texas westward to California and south through Mexico to Guatemala. It probably breeds in rodent nests. Modern specimens have been collected from packrat nests and from the fur of kangaroo rats, *Dipodomys* spp. (Brown 1939, Papp 1962). This beetle species was common in several assemblages from GLCA.

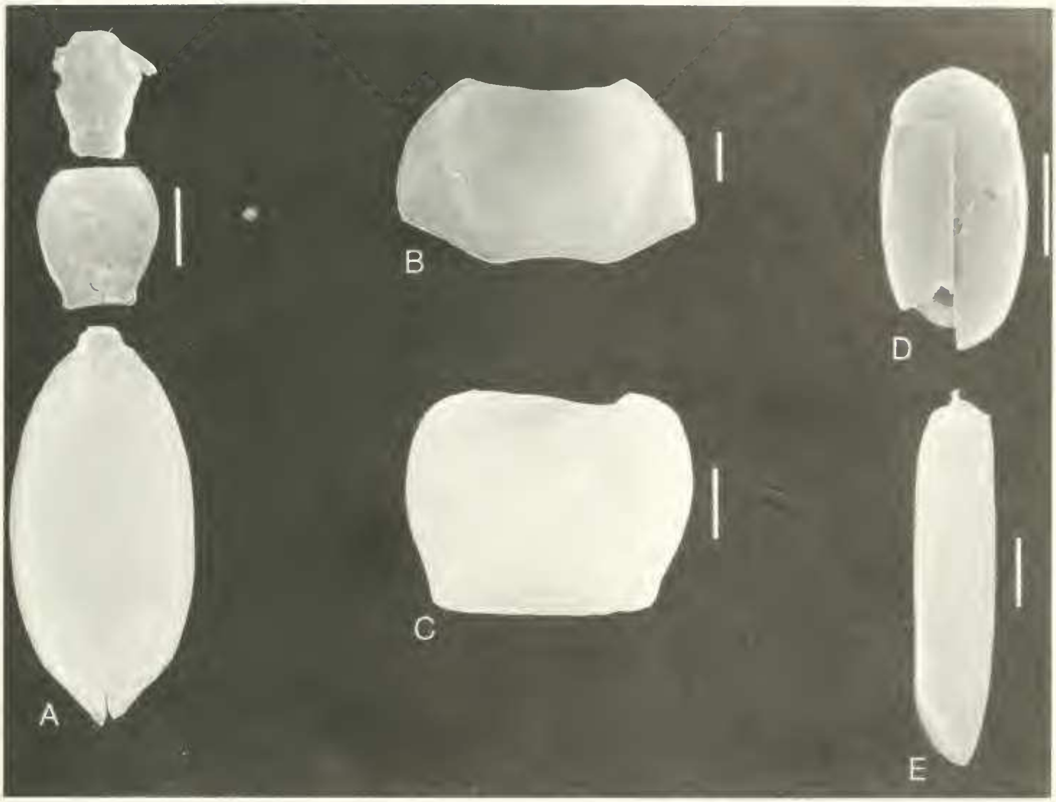

Fig. 2. Scanning electron micrographs of fossil beetles from sites discussed in text: A, head capsule, pronotum, and elytra of *Agonum perlevis* from the Bowns packrat midden, Glen Canyon; B, pronotum of *Thanatophilus truncatus* from Bida Cave, Grand Canyon; C, pronotum of *Elcodes nigrina* from Kaetan Cave, Grand Canyon; D, exoskeleton of *Anaspis rufa* from Bida Cave, Grand Canyon; E, left elytron of *Cymatodera pallida* from Hoodoo packrat midden, Canyonlands. Scale bar equals 1 mm.

The darkling beetle (Tenebrionidae), *Elcodes nigrina* (Fig. 2C), was found in a late Pleistocene assemblage from the GLCA. This scavenger is known today from the Pacific Northwest south to the mountains of Arizona. It is a cold-hardy species, found at elevations up to 3050 m in the Colorado Rockies (Blaisdell 1909).

The false darkling beetle (Melandryidae), *Anaspis rufa* (Fig. 2D), is widespread today. Beetles in this family are found under bark, in fungi, and in decaying logs (Liljeblad 1945).

The leaf beetle (Chrysomelidae), *Lema trilinea*, feeds on *Datura* (jimson weed) and other plants in the southern half of the United States. It was identified from a late Pleistocene assemblage in the GRCA. Other plant-feeding beetles identified from the fossil assemblages include the weevils (Curculionidae) *Scyphophorus acupunctatus*, *Orimodema protracta*, *Apleurus angularis*, and *Cleonidius trivattatus* or *C. quadrilineatus*, all from the Grand Canyon assemblage. Of these, *O. protracta* was found only in the late Holocene, *A. angularis* and *C. trivittatus* or *C. quadrilineatus* were found only in the late Pleistocene, and *S. acupunctatus* was identified from both periods. *O. protracta* lives at elevations from 2250 to 2700 m in the mountains of Arizona. It is a soil dweller that feeds on roots (R. S. Anderson, National Museum of Natural Sciences, Ottawa, written communication, July 1990). *A. angularis*, *C. trivittatus*, and *C. quadrilineatus* are all widespread today throughout western North America, while *S. acupunctatus* has been collected from Arizona and Mexico, where it feeds on *Agave*, *Dasylirion* (sotol), and *Lophophora* (peyote) (R. S. Anderson, National Museum of Natural Sciences, Ottawa, written communication, July 1990).

Finally, the tick (Ixodidae), *Dermacentor andersoni*, is found today in the western United States as far east as Montana. Immature

D. andersoni parasitize small mammals, while the adult stage parasitizes large mammals. This tick is a vector for Rocky Mountain spotted fever and Colorado tick fever (J. Keirans, National Institutes of Health, Bethesda, Maryland, written communication, June 1990).

PALEOENVIRONMENTAL INTERPRETATIONS

The information from the fossil insect record of the Colorado Plateau region is not yet sufficiently detailed to allow precise paleoenvironmental reconstructions. However, for both the Grand Canyon and Glen Canyon regions, the available insect data suggest a cooler, moister climatic regime during the late Pleistocene. Montane-adapted species lived at lower elevations. The insects document the presence of conifers at the sites but also suggest that a mosaic of vegetation types was locally represented, including grassland and shrubby terrain. The shift to postglacial climates occurred sometime after 14,000 yr B.P., and the most arid conditions appear to have developed within the last 1500 years. Additional studies of regional insect assemblages will undoubtedly clarify the nature and timing of environmental changes.

Although preliminary and incomplete in nature, the arthropod data presented here are in agreement with the detailed plant reconstruction provided by the macrobotanical remains from the packrat middens. Cole (1990) concludes that a comparison of modern and full-glacial assemblages from the eastern GRCA packrat middens demonstrates that individual plant taxa and comparable communities shifted upward approximately 800 m at the close of the Wisconsin glacial (ca 11,000 yr B.P.). Cole (1990) concludes that the climate at the elevations of Bida and Kaetan caves was more continental during the late glacial. This result is in contradiction to the equable climates that may have occurred in western and lower-elevation regions of the GRCA and to the south of the Colorado Plateau (Mead and Phillips 1981, VanDevender 1990). Our arthropod data presented here do little to clarify the continental vs. equable climatic reconstruction contradiction. Our "cooler, moister climatic regime" reconstruction could be interpreted as a continental climate; however, it could also represent a regime with slightly cooler winters and cool summers, and therefore more available moisture.

ACKNOWLEDGMENTS

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LITERATURE CITED

ANTEVS, E. 1939. Studies on the past climate in relation to man in the Southwest. Carnegie Institution of Washington Year Book 38: 317–319.

BARR, T. C. 1982. The cavernicolous anchomenine beetles of Mexico (Coleoptera: Carabidae: Agonini). Texas Memorial Bulletin 28: 161–192.

BETANCOURT, J. L., T. R. VAN DEVENDER, AND P. S. MARTIN. 1990. Packrat middens. The last 40,000 years of biotic change. University of Arizona Press, Tucson. 467 pp.

BLAISDELL, F. E. 1909. A monographic revision of the Coleoptera belonging to the Tenebrionidae tribe Eleodiini inhabiting the United States, lower California, and adjacent islands. Bulletin of the United States National Museum 63: 1–524.

BROWN, W. J. 1939. *Niptus* Boield. and allied genera in North America (Coleoptera: Ptinidae). Canadian Entomologist 91: 627–633.

COLE, K. L. 1990. Late Quaternary vegetation gradients through the Grand Canyon. Pages 240–258 *in* J. L. Betancourt, T. R. Van Devender, and P. S. Martin, eds., Packrat middens. The last 40,000 years of biotic change. University of Arizona Press, Tucson. 467 pp.

DAVIS, O. K., L. D. AGENBROAD, P. S. MARTIN, AND J. I. MEAD. 1984. The Pleistocene dung blanket of Bechan Cave, Utah. Pages 267–282 *in* H. H. Genoways and M. R. Dawson, eds., Contributions in Quaternary vertebrate paleontology: a volume in memorial of John E. Guilday. Carnegie Museum of Natural History Special Publication. 538 pp.

ELIAS, S. A. 1987. Paleoenvironmental significance of late Quaternary insect fossils from packrat middens in south-central New Mexico. Southwestern Naturalist 32: 383–390.

_______. 1990. Observations on the taphonomy of late Quaternary insect fossil remains in packrat middens of the Chihuahuan Desert. Palaios 5:356–363.

ELIAS, S. A., AND T. R. VAN DEVENDER. 1990. Fossil insect evidence for late Quaternary climate change in the Big Bend region, Chihuahuan Desert, Texas. Quaternary Research 34: 249–261.

_______. 1991. Insect fossil evidence of late Quaternary environments in the northern Chihuahuan Desert of Texas and New Mexico: comparisons with the paleobotanical record. Southwestern Naturalist. In press.

GIDASPOW, T. 1959. North American caterpillar hunters of the genera *Calosoma* and *Callisthenes*. Bulletin of the American Museum of Natural History 116: 227–343.

HANSEN, R. M. 1980. Late Pleistocene plant fragments in the dungs of herbivores at Cowboy Cave. Pages 179–189 *in* J. D. Jennings, ed., Cowboy Cave. Vol. 104. University of Utah Anthropological Papers.

LAUDERMILK, J. D., AND P. A. MUNZ. 1934. Plants in the dung of *Nothrotherium* from Gypsum Cave, Nevada. Carnegie Institution of Washington Publication 453: 31–37.

_______. 1938. Plants in the dung of *Nothrotherium* from Rampart and Muav Caves, Arizona. Carnegie Institution of Washington Publication 487: 271–281.

LILJEBLAD, E. 1945. Monograph of the family Mordellidae (Coleoptera) of North America, north of Mexico. Miscellaneous Publications of Zoology, University of Michigan 62:205–219.

MARTIN, P. S., B. E. SABELS, AND D. SHUTLER. 1961. Rampart Cave coprolite and ecology of the Shasta ground sloth. American Journal of Science 259: 102–127.

MCVICKAR, J. L., AND J. I. MEAD. Late Quaternary floras from Bida Cave and Kaetan Cave, Grand Canyon, Arizona. Unpublished manuscript.

MEAD, J. I. 1983. Harrington's extinct mountain goat (*Oreamnos harringtoni*) and its environment in the Grand Canyon, Arizona. Unpublished doctoral dissertation, University of Arizona, Tucson. 215 pp.

MEAD, J. I., AND L. D. AGENBROAD. Late Quaternary packrat midden floras from the central Colorado Plateau, southeastern Utah. Unpublished manuscript.

_______. 1989. Pleistocene dung and the extinct herbivores of the Colorado Plateau, southwestern USA. Cranium 6: 29–44.

MEAD, J. I., L. D. AGENBROAD, O. K. DAVIS, AND P. S. MARTIN. 1986. Dung of *Mammuthus* in the arid Southwest, North America. Quaternary Research 25: 121–127.

MEAD, J. I., L. D. AGENBROAD, A. M. PHILLIPS, AND L. T. MIDDLETON. 1987. Extinct mountain goat (*Oreamnos harringtoni*) in southeastern Utah. Quaternary Research 27: 323–333.

MEAD, J. I., P. S. MARTIN, R. C. EULER, A. LONG, A. J. T. JULL, L. G. TOOLIN, D. J. DONAHUE, AND T. W. LINICK. 1986. Extinction of Harrington's mountain goat. Proceedings of the National Academy of Science 83: 836–839.

MEAD, J. I., M. K. O'ROURKE, AND T. M. FOPPE. 1986. Dung and diet of the extinct Harrington's mountain goat (*Oreamnos harringtoni*). Journal of Mammalogy 67: 284–293.

MEAD, J. I., AND A. M. PHILLIPS. 1981. The late Pleistocene and Holocene fauna and flora of Vulture Cave, Grand Canyon, Arizona. Southwestern Naturalist 26: 257–288.

O'ROURKE, M. K., AND J. I. MEAD. 1985. Late Pleistocene and Holocene pollen records from two caves in the Grand Canyon of Arizona, USA. Pages 169–185 *in* B. Jacobs, P. Fall, and O. Davis, eds., Pleistocene and Holocene vegetation and climate of the southwestern United States. American Associate of Stratigraphic Palynologists Foundation Special Contribution Series 16.

PAPP, C. S. 1962. An illustrated and descriptive catalogue of the Ptinidae of North America. Deutsche Entomologische Zeitschrift 9: 367–423.

PECK, S. B., AND M. M. KAULBARS. 1987. A synopsis of the distribution and bionomics of the carrion beetles (Coleoptera: Silphidae) of the conterminous United States. Proceedings of the Entomological Society of Ontario 118: 47–81.

VAN DEVENDER, T. R. 1990. Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. Pages 134–165 *in* J. L. Betancourt, T. R. Van Devender, and P. S. Martin, eds., Packrat middens: The last 40,000 years of biotic change. University of Arizona Press, Tucson. 467 pp.

VAURIE, P. 1952. The checkered beetles of north central Mexico (Coleoptera, Cleridae). American Museum Novitates 1597: 1–37.

WILSON, R. W. 1942. Preliminary study of the fauna of Rampart Cave, Arizona. Contributions to Paleontology. Carnegie Institution of Washington Publication 530: 169–185.

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